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ATTACKS ON LARGE OR HEAVILY DEFENDED PREY BY TROPICAL SALTICID SPIDERS

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Introduction

Spiderlings in the first active instar have severe limitations in prey capture, because of their small size (Valerio, 1975) and particularly in those species that ambush or stalk their prey. The presence of snares or catching webs characteristic of several families expands considerably the range of potential prey items, which is undoubtedly an important pressure in the evolution of such structures. Even web-building spiders have problems with the large heavily-sclerotised prey items (see for instance Robinson & Robinson 1973a, 57–58). Insects with chemical defenses also prove troublesome to spiders (Eisner & Dean, 1976). However, the use of silk in the immobilization wrapping of araneid spiders considerably enhances their ability to subdue large or heavily defended prey (see experimental analyses summarized in Robinson 1975).

Salticids, on the other hand, are among the hunting spiders that subdue their prey without the aid of silk. For this reason, it is widely assumed that they are limited, in general, to prey which is smaller than themselves or to soft-bodied defenseless items (Enders 1975, 745 and references). At first sight this assumption seems perfectly reasonable, since the salticid attacking prey larger than itself must contend with a strength (perhaps) superior to its own. The insect under attack would presumably push against the substrate and exert sufficient pressure either to escape or to injure

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the spider. We here report on field observations (in Panama and Costa Rica) that show that certain tropical salticids do attack and subdue prey considerably larger than themselves. Among these prey are large araneid spiders that are attacked on the web (but not *across* the web). In making these attacks on large prey the spider may utilize the technique of dropping on its dragline to isolate such prey from the substrate. This action allows the spider to safely attack other types of prey which, although small, are normally protected by social defenses.

Observations

An adult *Phiale* was observed in Panama, preying upon a fully sclerotised adult dragonfly that was at least three times as long as the spider. The spider was on the upper surface of a leaf about 1.5 meters above ground level. At the time of discovery the dragonfly was fluttering spasmodically but the actual capture was not observed. There is little doubt that the dragonfly was attacked after alighting on the leaf. The relative proportions of the spider and its prey are obvious from the photograph (Figure 1.).

Observations in the Central Valley, Costa Rica, provide a clue about how small salticids may subdue large prey. An immature *Menemerus bivittatus* was seen pouncing on a large moth resting on a fence wire. The moth was about half as long again as the spider and perhaps twice as heavy. After the pounce the moth started beating its wings strongly and the spider immediately dropped, on its dragline, until it was well clear of the substrate (figure 2). The spider held the moth with its chelicerae and front legs until the prey was subdued.

Clearly this method of "playing" the prey on the end of a line until envenomation occurs or the prey is exhausted, or both, is a strategy that could be applied to any prey item that tried to escape from the spider by jumping, dropping or flying off the substrate. The tensile strength of the dragline silk, in all probability, greatly exceeds the load exerted by the spider and her prey. The tenacity of the spider's jaw hold may be the critical factor in such attacks.

Dropping below the substrate on a dragline also provides the spider with an effective method of dealing with some species of ants that have social defenses. Thus some species of *Pseudomyrmex* possess a strong alarm pheromone that directs large numbers

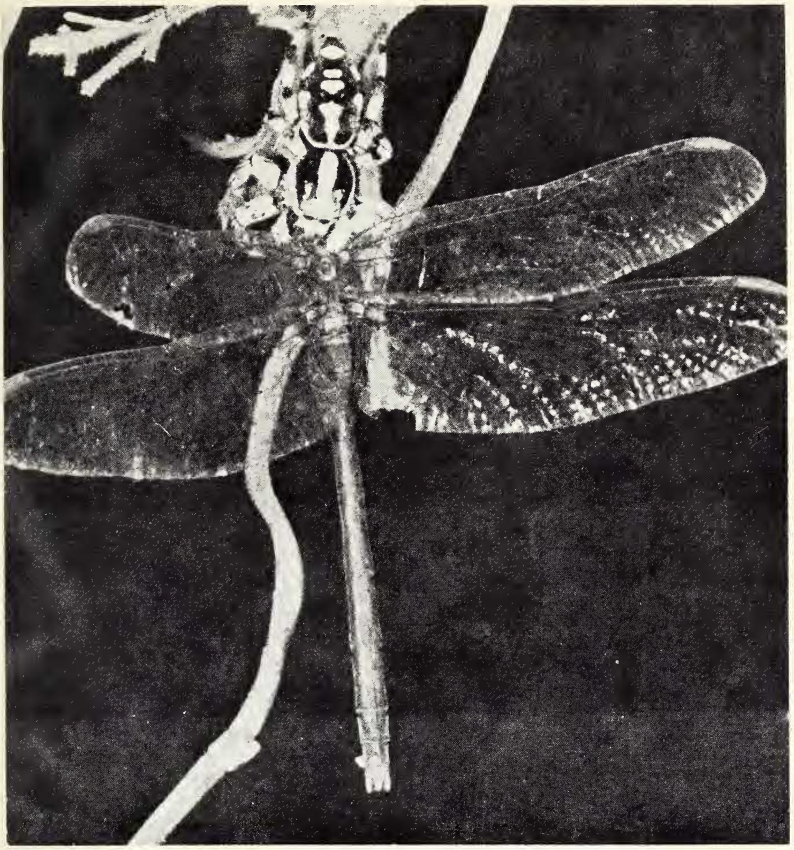

Figure 1. Adult female *Phiale* sp. feeding on anisopteran dragonfly, Navy Pipeline Road, Canal Zone, Panama. June 18th 1976.

of individuals to the exact place where a member of their colony is in danger. The response to the alarm pheromone is very rapid and may occur within seconds (Janzen 1966). This adaptation could effectively deter salticid predation on the ants were it not for the use of the dragline described above. An unidentified salticid (not collected) was observed making effective use of this technique at a lowland site in Guanacaste, Costa Rica. The *Pseudomyrmex* were attacked in an *Acacia* tree. The spider simply pounced on the ant, dropped off the branch and held the ant, suspended on the end of the dragline, and ate it. The ants, attracted by the

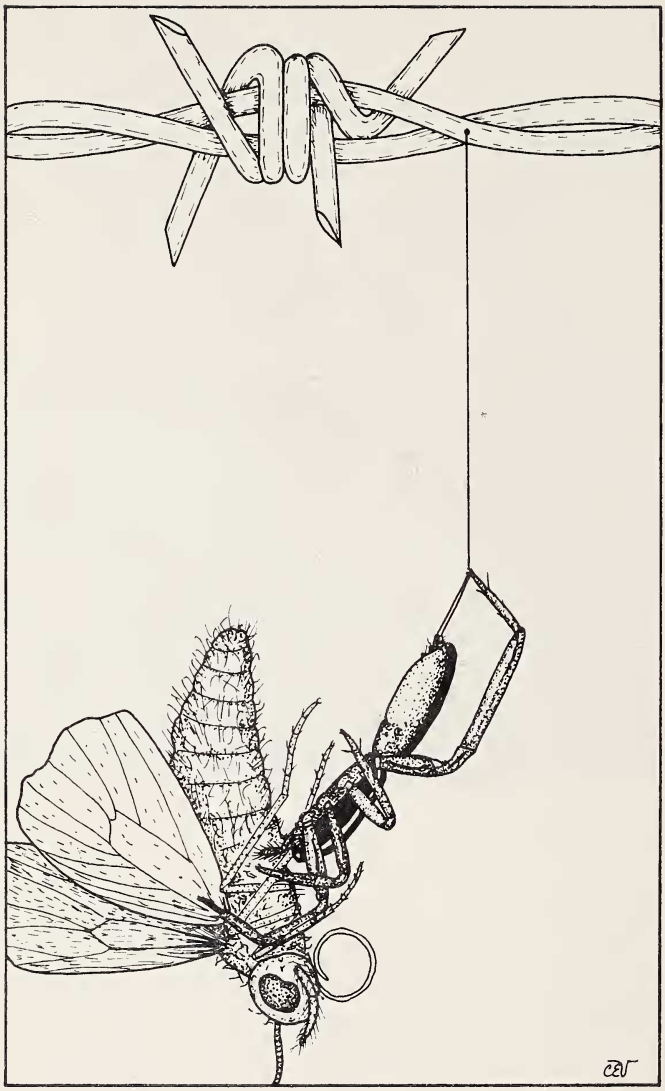

Figure 2. Immature *Menemerus bivittatus* feeding on moth in Central Valley, Costa Rica. The spider has dropped on its dragline beneath the fencing wire.

alarm pheromone, found the end of the dragline, but were unable to descend the thread. The spider returned to the branch and repeated the operation several times during the period of observation. (It is worth noting that at night we frequently find salticids and other diurnal non-web-building spiders suspended on their draglines beneath the vegetation. This may provide the safest way of spending the hours of darkness, since they are virtually isolated from the vegetation on which prowl innumerable predatory arthropods. Should any of these be capable of descending the dragline, the vibrations thereby induced would presumably alert the resting spider.)

Attacks on web-building spiders.

There are indications that web-building spiders are preyed upon by an extensive array of predators although the records are scattered throughout the literature and detailed observations are surprisingly few in number. Bristowe (1941; 331–443) deals comprehensively with the enemies of spiders in general and also describes a wide variety of anti-predator adaptations that spiders possess. The defenses of tropical orb-weavers are reviewed by Robinson & Robinson (1970; 649–653) and these authors describe particular defensive structures or behaviors elsewhere (1973a, 1973b). Tolbert (1975) has reviewed some of the available literature on araneid defensive behaviors in conjunction with an experimental study of the defensive responses of *Argiope aurantia* and *A. trifasciata.*

Records of attacks on orb-weavers by other spiders have been few in number. Bristowe (1941; 377–378) lists a number of attacks on web-building spiders by hunting spiders, and, in particular, by the salticid *Linus fimbiatus.* The spiders attacked included at least one araneid. Bristowe (ibid; 378) implies that the spiders were captured in their webs, "The *Linus* . . . sat in its victim's web to eat the owner". Tolbert (1975) mentions attacks on *Argiope aurantia* and *A. trifasciata* by salticids and states that attacks in the field can be induced by prodding the *Argiope* to move (Tolbert, in litt.). Enders (1974) reports attacks on orb-weavers by orb-weavers and (1975; 970) on the "invasion" of the webs of orb-weavers by errant salticids.

In three months (May–July, 1976) during extensive censusing of webs in a number of forest fringe habitats in the Summit

and Gamboa areas of the Panama Canal Zone, 14 adult female *Argiope argentata* were found being consumed by *Phiale* adults. (On one count *Phiale* were found consuming 3 out of 64 spiders censused.) The spiders were, in all cases, off the web and resting on nearby vegetation. The araneid is considerably larger than the salticid (figure 3) and at least twice as heavy. A *Phiale* was also seen feeding on a late instar *Nephila clavipes* (F. Vollrath, pers comm.). No attacks were seen and it was not clear how the salticid had captured the araneid. To settle this problem, salticids were introduced into cages containing adult *A. argentata* (in webs) and watched. The web-builders were not fed and no attacks or "invasions" of the web were seen during intermittent observations over a period of three days. Feeding one spider immediately gave a clue as to the attack method of the salticid. As the *Argiope* moved to attack a grasshopper the salticid became active and moved along the walls of the cage to various positions from which it clearly "looked" at the moving *Argiope*. No attack was made, but when the spider returned to the hub, leaving the wrapped prey at the capture site, the salticid moved to a position on the cage wall almost horizontally opposite the stored prey, and after a number of side to side movements of the cephalothorax, it leapt upon the prey to stand astride it, biting. The *Argiope* immediately started to make *pumping* movements at the hub ('web-flexing', Tolbert 1975). This movement shook the prey item and shortly after its commencement, the salticid jumped off and regained its former position on the cage wall. Feeding the same spider a second time resulted in a similar response on the part of the salticid. This time, after leaping on the completely motionless prey package, it did not provoke the *Argiope* into pumping, and fed undisturbed on the cricket for over five minutes. At this point the host ran to the stored prey and dragged it closer to the hub, and the salticid leapt off to regain the cage wall. The salticid made one more attack on the prey package and then 16½ minutes after the start of the activity, attacked the spider at the hub by leaping on it. The *Argiope* was on the opposite side of the hub to the salticid and immediately dropped to the cage floor. The *Phiale* then walked on the web to the stored prey and fed upon it. Subsequent experimentation showed that the salticids could regularly be induced to attack *Argiope* if the latter were provoked into moving. Attacks on the wrong side of the hub were not successful

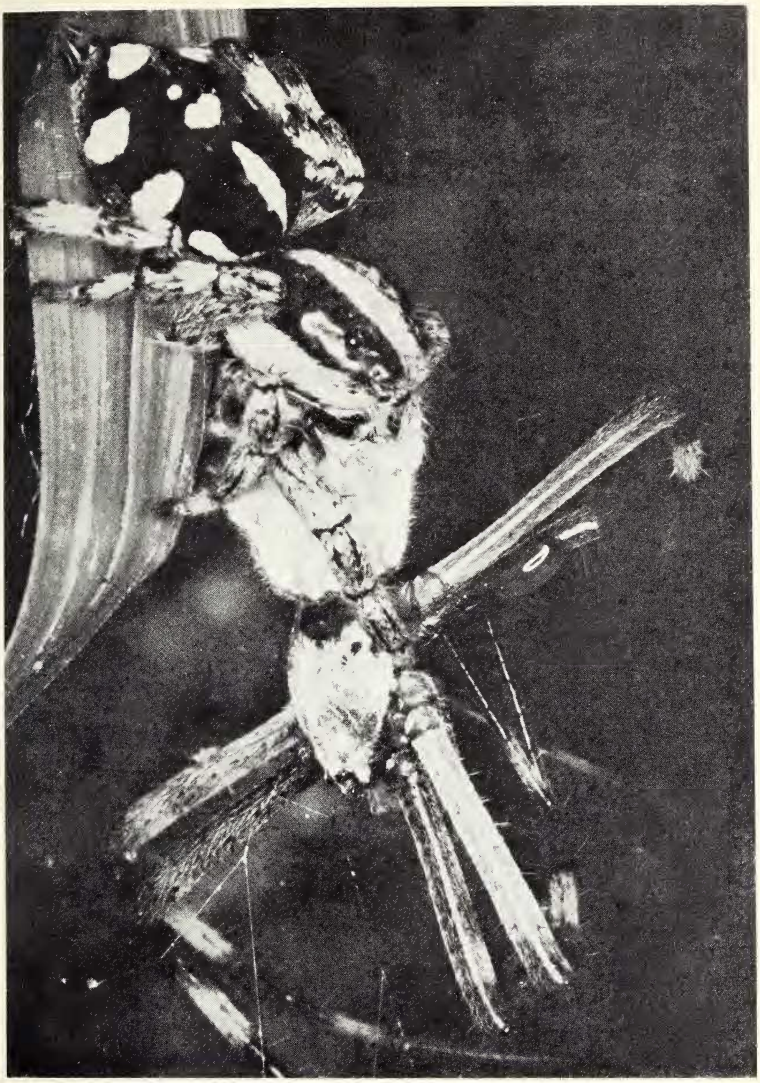

Figure 3. Adult female *Phiale* sp. feeding on adult female *Argiope argentata*. The salticid is perched close to the upper left hand corner of the araneid's web. Old Gamboa Road, Canal Zone, Panama. May 19th 1976.

but attacks from above the dorsal surface of the araneid were successful in all cases. (Eventually, all four *A. argentata* were killed.) In all cases, the araneids jumped off the hub when the *Phiale* contacted them. At the cage floor they moved about but could not displace the salticid and were eventually pulled up the cage wall to a feeding site.

The conditions in the cages probably made the attacks easier than they would be in field conditions. The *Argiope* web was surrounded by a continuous rigid surface on all sides. In the field the salticid must have to rely on discrete vegetation units for originating its attacks and though it can jump from plant to plant until it finds a suitable site, it may not be able to keep the spider in view continuously. In the cages the salticids looked at the *Argiope* from the cage floor, the cage walls and even the cage roof, before eventually lining up on the wall to launch an attack. Where it was possible to gauge the point of origin of attacks with some accuracy, they seemed to occur from a position only slightly above the point horizontally opposite the spider. When launching attacks off the glass sides of cages, the salticid turned around several times before jumping. Subsequent examination showed several silk attachments on the glass in this region. This suggests that the spider may make multiple dragline attachments before long aerial attacks. Take off postures were always head down (i.e. with the cephalothorax lowermost but strongly angled towards the target, and with legs I off the substrate).

These observations made on a small sample in simplified conditions show that an attack on the dorsal surface of a large prey item can be very successful. Movement seems to be necessary for the initiation of hunting behavior, but attacks were made on subsequently motionless prey. The salticids made accurate distance terminations and traversed horizontal distances measured at greater than 12cm. The failure of attacks made from the 'wrong side of the hub' (i.e. with the web between the salticid and the araneid) suggest that the behavior of *shuttling* (= switching sides of the web, Tolbert 1975), may be an effective defense, as argued by Robinson & Robinson (1970). Dropping from the web clearly did not aid the araneid in the experimental situation but could help in defense against salticids in a more natural one. The araneid might be able to brush off its attacker against the vegetation below the web. It can clearly work in other contexts against other predators.

The basic predatory techniques.

Dropping on the dragline to isolate a large prey from the substrate may be partly fortuitous in some cases. Certainly it depends on the prey moving off the substrate as a result of its own escape movements, since the salticid cannot lift it off. However, the case of the attacks on the ants suggests that it may be part of the normal predatory repertoire for dealing with some types of small prey. Attacking large araneids from above their dorsal surface presumably utilizes a technique that is part of normal prey capture but capitalizes on the araneid's inability to make strong scraping movements against its upper surface. It is also probable that such attacks benefit from the fact that the spider is not standing on a rigid substrate when attacked. The peculiar defensive posture adopted by *Nephila* spp. in response to direct tactile stimulation of their dorsal surfaces (Robinson & Robinson 1973a) results in a "barrier" of flexed legs being erected above the spider and could serve to frustrate some dorsal attacks.

Summary

1. Some tropical salticids regularly catch prey larger and heavier than themselves.
2. Such salticids may utilize a dorsal attack on the prey followed by dropping on a dragline to effectively isolate the prey from the substrate.
3. This technique could be much more common than we know and definitely extends the size range for the potential prey of these spiders.
4. The drop and hold technique allows the salticids to attack prey that would normally be protected by social defense.
5. Salticids can make aerial attacks on araneid spiders in their webs and the normal defensive dropping responses of these spiders may, in certain circumstances, facilitate the salticid attack.

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